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Distribution and abundance of exotic earthworms within a boreal forest system in southcentral Alaska

Deanna Marie Saltmarsh[1], Matthew L. Bowser[2], John M. Morton[2], Shirley Lang[3], Daniel Shain[3], Roman Dial[1]

1 *Department of Environmental Science, 4101 University Drive, Alaska Pacific University, Anchorage, AK 99508, USA* **2** *US Fish and Wildlife Service, Kenai National Wildlife Refuge, Soldotna, AK 99669, USA* **3** *Biology Department, 315 Penn St., Rutgers The State University of New Jersey, Camden, NJ 08102, USA*

Corresponding author: *Matthew L. Bowser* (matt_bowser@fws.gov)

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Abstract

Little is known about exotic earthworms (Oligochaeta: Lumbricidae) in Alaska outside its southeastern panhandle. This study documents the distribution of exotic earthworms in the relatively undisturbed Kenai National Wildlife Refuge (KNWR), a large, primarily wilderness refuge in southcentral Alaska. We sampled 69 sites near boat launches, along road corridors, and in low human impact areas > 5 km from the road, finding three species of earthworms (*Dendrobaena octaedra*, *Dendrodrilus rubidus*, and *Lumbricus terrestris*). Most road sites (90%) and boat launches (80%) contained earthworms; half (50%) of low human impact sites contained earthworms. Distance to roads was the only significant factor in predicting earthworm occurrence; soil pH, soil moisture, leaf litter depth, and vegetation cover were not. The disparate distributions of these three species suggest that within the KNWR road construction and vehicle traffic played a role in dispersal of the widespread, abundant *Dendrobaena octaedra* and uncommon *Dendrodrilus rubidus*; bait abandonment appeared to be the primary method of introduction of *Lumbricus terrestris*. While the distribution of harmful anecic earthworms in KNWR is currently limited, the prohibition of *Lumbricus* spp. as bait within conservation units in Alaska may be warranted.

Keywords

Lumbricidae, earthworm invasion, taiga, bait abandonment, non-native species

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Introduction

Pleistocene glaciations extirpated native earthworms from much of North America, leaving landscapes devoid of earthworms until the introduction of exotic earthworms (Oligochaeta; Lumbricidae) during European settlement (Hale et al. 2005, 2006, Frelich et al. 2006, Holdsworth et al. 2007a, 2007b). The effects of exotic earthworms on forest ecosystems are well documented (Hale et al. 2005, 2006, Frelich et al. 2006, Holdsworth et al. 2007a, 2007b) and vary by feeding strategy. Leaf litter-dwelling, small-sized epigeic species are least destructive, consuming and mixing the top organic layers into textured, homogeneous litter. Endogeic species burrow through the top soil horizon; their physical effects on ecosystem ecology are greater than epigeic worms but less than anecic worms. Anecic earthworms penetrate deep into the soil, transporting surface litter into the mineral layer (Addison 2008) and increasing soil porosity and water infiltration (Anderson 1988). Removal of leaf litter and deposition of casts on the soil surface by anecic earthworms can also increase soil erosion and nutrient run-off (Edwards and Bohlen 1996).

Material transport by anecic worms, their large adult size, and dense populations have led to substantial ecosystem changes in some parts of North America (Frelich et al. 2006). Earthworms can accelerate litter decomposition (Hale et al. 2006, Suárez et al. 2006, Holdsworth et al. 2007a, 2007b, Addison 2008) and reduce plant species richness (Hale et al. 2006, Holdsworth et al. 2007a, 2007b). Suárez et al. (2006) found that litter remaining in earthworm-invaded areas in New York was 30-60% less than in reference plots. Holdsworth et al. (2007a) found in a Wisconsin forest that exotic earthworms reduced plant species richness in heavily invaded plots by 17%. Similarly, Hale et al. (2006) documented a negative relationship between exotic earthworm diversity and plant diversity in a Minnesota hardwood forest.

Most studies of exotic earthworms have occurred in temperate regions (Hale et al. 2006, Suárez et al. 2006, Holdsworth et al. 2007a, 2007b, Addison 2008); less is known about the distribution and effects of earthworms in subarctic boreal forests (Cameron et al. 2007, Cameron and Bayne 2009, Sanderson et al. 2012). In northern Alberta, Cameron et al. (2007) found boat launches and roads had the highest probability of earthworm occurrence. Their results suggested vehicle transport and bait abandonment as primary mechanisms of earthworm introduction.

As for most invasive species, human activities, particularly road construction and unintentional transport, likely increase the rate of spread for exotic earthworms above their natural dispersal rate of 5-10 meters a year (Gundale et al. 2005, Addison 2008). Consequently, exotic earthworms more likely occur near roads due to availability of habitats disturbed by road construction and maintenance that allow for potential establishment, as well as the creation of dispersal corridors (Cameron et al. 2009). Vehicles themselves function as dispersal vectors for earthworm cocoons, which are sticky, mucus coated sacks containing developing embryos (Gundale et al. 2005). Several species such as *Lumbricus terrestris* (anecic) and *Lumbricus rubellus* (epi-endogeic) are sold commercially as fishing bait and are possibly introduced into ecosystems when anglers discard unused bait (Cameron et al. 2007).

Seventeen species of earthworms are known to occur in Alaska (see records in Gates 1972, 1974, Reynolds et al. 1974, Reynolds and Wetzel 2008, Reynolds 1977, 1980, Berman and Marusik 1994, Costello et al. 2011, Rinella et al. 2014, and Suppl. material 1: Alaska earthworm records). Of these, 14 are exotic worms introduced from the Palearctic and have become established. *Eisenia fetida* (Savigny, 1826), a Palearctic species, is commonly used for indoor vermicomposting in Alaska, but due to its low cold tolerance (Greiner et al. 2011, Meshcheryakova and Berman 2014), it is unlikely to become established in Alaska. Two species of earthworms found in southeast Alaska (*Arctiostrotus* sp. and *Sparganophilus* sp.) may be native to Alaska or may have been transported from elsewhere in North America.

Factors such as pH and temperature likely limit earthworm distribution, especially in boreal regions like Alaska (Chan and Mead 2003, Addison 2008). Earthworms are usually associated with soil pH of 5-7.4, although *D. octaedra* inhabits soil pH as low as 2.8-3.6, and *L. rubellus* has been found in areas with pH ≥ 3.0 (Addison 2008). Survival of earthworms in low temperature areas depends on the species and stage of development (Greiner et al. 2011, Meshcheryakova et al. 2014). Meshcheryakova and Berman (2014), by comparing cold hardiness and present distributions of earthworm species in Siberia, concluded that varying cold tolerance of the species considered contributed toward their present distribution ranges.

A rapidly warming climate in Alaska is likely improving environmental conditions for earthworms. Wetlands in Alaska are warming and drying (Klein et al. 2005, Riordan et al. 2006, Berg et al. 2009) and average winter temperatures have warmed 3.5 °C in the last 50 years (Karl et al. 2009). Drying wetlands and warmer winters may provide increasingly suitable habitat for exotic earthworms. Addison (2008) suggested that even small increases in winter temperatures will lead to large increases in earthworm habitat.

The present study documents species composition, distribution, and habitat correlates for earthworms in the Kenai National Wildlife Refuge, a conservation area in southcentral Alaska. A secondary goal is to examine relationships between earthworm occurrence and distance from human-disturbed areas, such as roads and popular fishing areas. The final goal is to identify factors potentially limiting earthworm distribution, such as pH and soil moisture, which are likely to change as the climate continues to warm on the Kenai Peninsula.

Methods

Study area

Located on the Kenai Peninsula in southcentral Alaska, USA (60°N, 150°W), the Kenai National Wildlife Refuge (KNWR) covers 777,000 ha. Mountains and glaciers characterize the southeastern KNWR (Figure 1). The Kenai Lowlands, mantled by glacial deposits that vary in texture and are capped by silt loam derived from post-

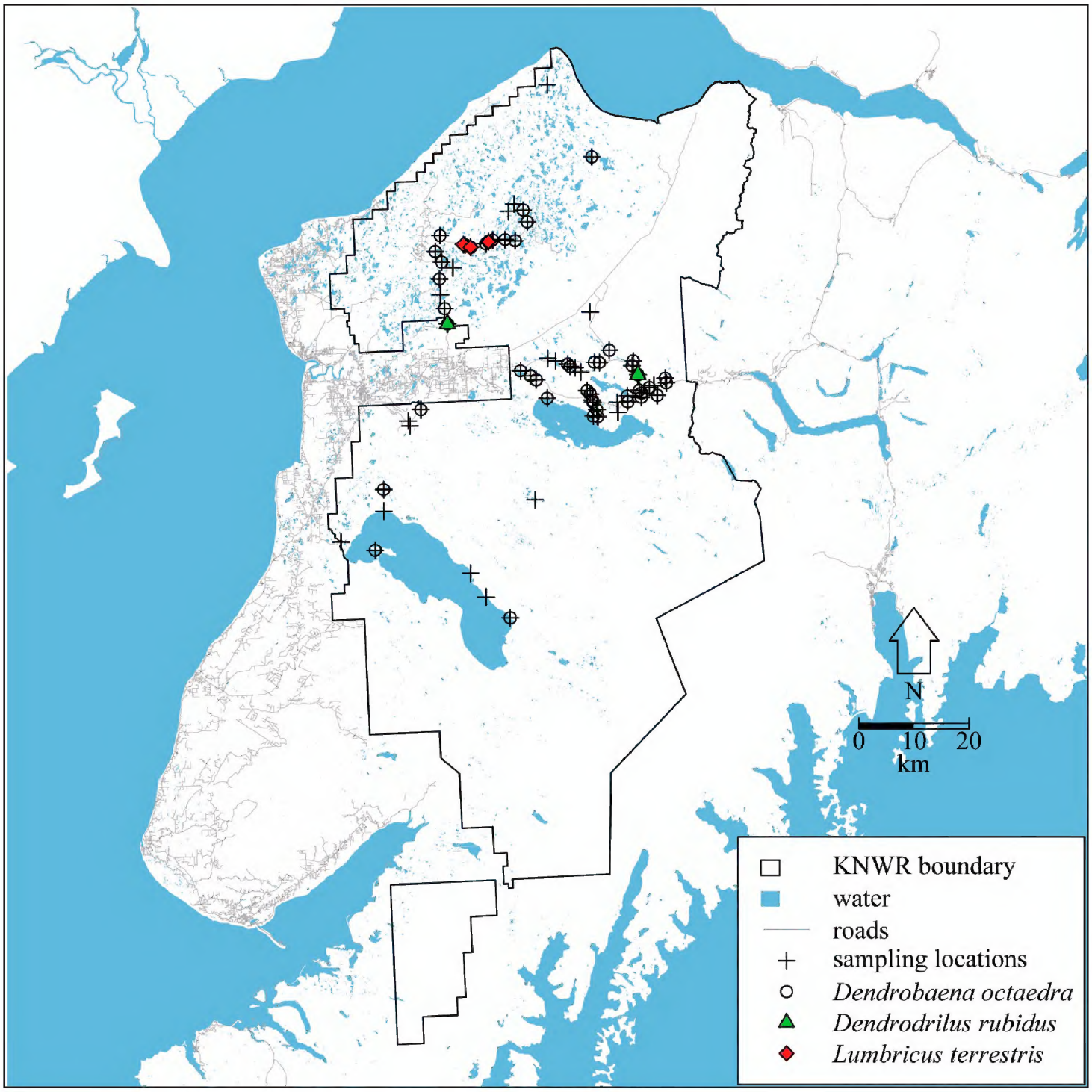

Figure 1. Map of sampling locations and earthworm occurrences by species.

glacial windblown loess, cover the western portion of KNWR. The Lowlands consist of wetlands and mixed boreal forest (Klein et al. 2005) dominated by black spruce (*Picea mariana*), white spruce (*Picea glauca*), birch (*Betula papyrifera*), and quaking aspen (*Populus tremuloides*). The climate is boreal with a maritime influence. Temperatures are rarely greater than 26 °C in summer or less than -18 °C in winter. The frost-free growing season varies from 71-129 days depending on location, with about 480 mm of total precipitation per year (U.S. Fish & Wildlife Service 2010).

While most of the KNWR is currently managed as congressionally designated Wilderness, over 130 historic cabins have been inventoried on the Refuge along with other historic resources associated with mining, trapping, oil development, and road construction, mostly in the north of the refuge. Commercial mining and fishing in the area occurred in the late 1800s and early 1900s. Oil exploration began in the northern

part of KNWR in the Swanson River area in the mid-1950s, resulting in 2,900 km of bulldozed seismic lines. There are also 240 km of utility and transmission lines and 180 km of established trails within the Refuge (U.S. Fish & Wildlife Service 2010). Fire and associated suppression activities have also been prevalent within the refuge in the past. Major fires of unknown origin occurred in 1871, 1883, 1891, and 1910. Two large, human-caused fires (1947: 125,000 ha and 1969: 35,000 ha) resulted in replacement of mature spruce forests by a mosaic of young mixed conifer-deciduous forest in various stages of succession. Many historic disturbances provided opportunities for earthworm introduction and establishment on the KNWR.

Experimental design

Earthworms were sampled throughout the KNWR during July and August 2011 at 69 total sites representing three levels of human impact. These levels of human impact were characterized by explicit vectors of introduction: (1) boat launches (n = 20), (2) road corridors (n = 20); and (3) low impact areas (> 600 m from any road or facility and 50 m from any trail or river; n = 29). The sampling site locations were chosen within a GIS (ArcGIS v.10.1) by first identifying suitable areas for each impact level and then randomly selecting sample sites. Three 0.09 m^2 plots were established at each site to sample earthworm occurrence. At road and boat launch sites, plots were placed two, three, and five meters from the road or edge of a boat launch. The plots were located approximately 10 m apart when possible, establishing a wider area for detecting earthworm occurrence. This protocol was modified at four of the low impact sites accessed by float plane, where only a single 0.09 m^2 quadrat was sampled at each site.

Plot level sampling

We sampled earthworm abundance at each plot using a 30 cm × 30 cm quadrat. Within each quadrat we removed and hand-sorted surface organic material for earthworms. We extracted additional earthworms with a liquid mustard solution of 40 g ground mustard powder in 3.8 L water (Lawrence and Bowers 2002). Earthworms were collected and stored in 70% ethanol. Specimens were deposited in the entomology collection of the Kenai National Wildlife Refuge (coden: KNWR) and specimen data were made available via Arctos (http://arctos.database.museum/).

We identified earthworm specimens to species level when possible based on visual observations of external morphology (Reynolds 1977). Juveniles were grouped into two categories: (1) *Lumbricus* spp. and (2) other immature. In addition, six specimens collected at geographically remote sites were identified to species level using the mitochondrial COI barcoding gene to confirm taxonomic identification using the Basic Local Alignment Search Tool (BLAST) and the BOLD identification engine (http://www.boldsystems.org). We submitted sequence data to BOLD where they are publicly available.

We measured leaf litter depth by clearing a small area and measuring the vertical depth of the leaf layer with a 30 cm ruler within each plot. Soil pH, (Soil pH Meter, HANNA, RI), and moisture (Digital Moisture Meter, General, NY) were measured in the field. In each plot, we estimated the percentage cover of litter, grass, forbs, moss, and lichen. General forest type (deciduous, mixed, conifer) of the area was determined from field observations and a GIS land cover layer.

We estimated ash-free dry biomass (g) from the length (mm) of each preserved specimen with the allometric equation of Hale (Hale et al. 2004):

$$g = e^{2.2853\ln(mm)-11.9047}$$

Hale (2004) found that the allometric equations for *Octolasion tyrtaeum*, *Lumbricus* spp., and *Dendrobaena octaedra* were not significantly different from one another, allowing one equation for all species.

Lumbricus spp. distribution sampling

Anecic *Lumbricus* species are potentially more damaging than other genera (Eisenhauer et al. 2007). Consequently, at sites where *Lumbricus* spp. were found, we used three transects to estimate the extent of local distribution. One transect was perpendicular to the initial site and the other two at approximately 45 degree angles from the site. At 10 m intervals along each transect we sampled three plots for earthworm presence using liquid mustard extraction within a 0.25 m^2 quadrat. To delineate the boundaries of this infestation, we continued sampling until we failed to find earthworms in all three plots at two consecutive 10 m intervals. Earthworms were collected and stored in 70% ethanol and later identified in the lab.

Statistical analysis

Individual plots served as replicates for each site, but we used site level data for most analyses by averaging plot level data. A site was considered to contain earthworms if individuals were detected in at least one plot. Soil moisture and leaf litter depth were square-root transformed for normality. We calculated remoteness for each site as a measure of distance from the nearest road. This distance, Y (m), was calculated in GIS by using true surface distance, as it accounted for elevation changes and also masked out lakes. To approximate a normal distribution for analyses, we transformed this distance using $\ln(Y + 1)$.

All analyses were performed using R, version 3.1.2 (R Core Team 2014). We assessed independence of earthworm presence and human impact level (road, boat launch, low impact) and vegetation type (conifer, deciduous) using chi-square tests of independence. Correlations of independent variables were examined with the corr.test function of the psych package, version 1.5.1 (Revelle 2015), accepting default arguments.

Prior to occupancy modeling, principal components analysis (PCA) was used to reduce the dimensionality of the eight habitat variables soil pH, soil moisture, leaf litter depth, and moss, grass, lichen, litter, and forb cover percentages. PCA was performed using the PCA function from the FactoMineR package (Husson et al. 2015), version 1.29. We used the estim_ncp function, also from the FactoMineR package, to determine the optimal number of dimensions to use in the PCA.

Results of the PCA were included in occupancy models (MacKenzie et al. 2003, 2006) using the occu function of the unmarked package, version 0.10-4 (Fiske and Chandler 2011). Detection probability was assumed to be constant. Site occupancy was modeled using all 2^5=32 permutations of first-order terms for impact level (factor with three levels), forest type (factor with two levels), distance to roads, and values from the first two PCA components. Finally, we obtained parameter importance and AICc model-averaged estimates of coefficients of the independent variables from the full set of candidate models using the importance and modavg functions from the AICcmodavg package, vesion 2.0–3 (Mazerolle 2015).

We used MANOVA to determine the effects of the impact level and earthworm occurrence on the three dependent variables of soil pH, soil moisture, and leaf litter depth.

Results

Distribution and abundance

We found three exotic earthworm species, *Dendrobaena octaedra*, *Dendrodrilus rubidus*, and *Lumbricus terrestris*, on KNWR. We failed to detect *Lumbricus rubellus*, known from one location on KNWR (http://arctos.database.museum/guid/KNWR:Ento:6755), even though one of our sampling sites was only ~ 48 meters from this known occurrence. Specimen records are included in Suppl. material 2: Specimen records.

The six individuals that were genetically identified using the COI gene showed > 96% probability of identity to their respective species based on a BLAST results. BOLD process ID's for sequenced specimens are also included in Suppl. material 2: Specimen records.

No site had more than two species confirmed as present. Only four sites (three boat launch sites one road site) contained two species of earthworms, while the majority of sites contained only one species. *Dendrobaena octaedra* was the most widespread, occurring at 48 (70%) of 69 sites. Most immature earthworms appeared to be *D. octaedra* based on morphology. *Dendrodrilus rubidus* occurred at two sites geographically distant from one another. *Lumbricus terrestris* occurred at three sites, all of which were boat launches located adjacent to one another in the northern part of the Refuge (Figure 1). Along transects surveyed at these sites, we found that *L. terrestris* had dispersed only 30 to 110 m from the boat launches.

Overall, earthworms occurred at 49 (71%) of the 69 sampled sites. Nearly all road sites (18 of 20 total sites, 90%) had earthworms in at least one plot, as did most boat

launches (17 of 20 total sites, 85%). In contrast, only half (14 of 29 total sites, 48%) of the low-impact sites contained earthworms.

Earthworms occurred more frequently at roads and boat launch sites than expected, but much less frequently at low impact sites than expected (Table 1, chi-square test of independence, $\chi^2 = 11.18$, df = 2, p = 0.004, $n = 69$ observations). Earthworms were found more frequently than expected at sites dominated by deciduous trees and shrubs and less frequently than expected at conifer-dominated sites ($\chi^2 = 13.3$, df = 1, p = 0.0003, $n = 65$, Table 2).

Where earthworms were present, the mean density of earthworms was (28.1 ± 4.4 individuals/m^2), with mean densities ranging from 23.9 ± 4.5 at road sites to 33.1 ± 6.1 at boat launches (Table 3). At the three sites where transects were surveyed for *L. terrestris*, the mean density of this species was 37.4 ± 7.0 individuals/m^2. Log-transformed total earthworm densities (excluding absences) did not differ significantly among impact levels (one-way ANOVA: F = 1.57, $p = 0.219$).

Table 1. Observed and expected values for earthworm occurrence in boat launch, road, and low impact sites from a chi-square test of independence.

	Boat launch	Road	Low impact
Earthworms present	16 (13.9)	18 (13.9)	14 (20.2)
Earthworms absent	4 (6.1)	2 (6.1)	15 (8.8)

Table 2. Observed and expected values for earthworm occurrence at sites in conifer forests and deciduous trees/shrubs from a chi-square test of independence.

	Conifer	Deciduous
Earthworms present	7 (13.3)	41 (34.7)
Earthworms absent	11(4.7)	6 (12.3)

Table 3. Mean densities (individuals extracted/m^2 ± SE) by species and human impact level.

Species	Boat launch	Road	Low impact	Total density
Dendrobaena octaedra	26.4 ± 6.4	23.9 ± 4.5	26.9 ± 11.9	25.6 ± 4.4
Dendrodrilus rubidus	3.7 ± 3.7	7.4 ± 7.4	-	5.6 ± 1.9
Lumbricus terrestris	7.4 ± 7.4	-	-	7.4 ± 7.4
Unidentified immatures	43.2 ± 3.2	-	-	43.2 ± 3.2
Total density	33.1 ± 6.1	24.3 ± 4.7	26.9 ± 11.9	28.1 ± 4.4

Table 4. Mean biomass (mg/m^2 ± SE) of earthworms by species and human impact level.

Species	Boat launch	Road	Low impact	Total
Dendrobaena octaedra	105 ± 30	114 ± 19	193 ± 61.4	135 ± 23
Dendrodrilus rubidus	32.4	52.8	-	42.6 ± 10.2
Lumbricus terrestris	5651	-	-	5651
Unidentified immatures	1891	-	-	1891
All species	652 ± 353	105 ± 36	193 ± 61.4	361 ± 144

Where earthworms were found, ash-free dry biomass (AFD) of earthworms showed moderate variation (0.36 ± 0.14 AFD g/m^2, n = 49; Table 3) and was greatest at boat launches due to the presence of *Lumbricus* (0.65 ± 0.35 g/m^2, n = 16), lowest at roads (0.11 ± 0.04 g/m^2, n = 18), and moderate at low impact sites (0.19 ± 0.06 g/m^2, n = 14). At the three sites where transects were surveyed for *L. terrestris*, the mean AFD of this species was 4.2 ± 1.8 g/m^2. Log-transformed total earthworm biomass did not differ significantly among impact levels (one-way ANOVA: F = 0.818, p = 0.448). In summary, we found the highest density and biomass of earthworms at boat launches, and the least of both abundance metrics along roads.

PCA and occupancy modeling

There were many significant correlations among the habitat variables (Table 5). Depending on the method used for determining the best number of principal components to include, the optimal number was estimated to be two or three. We chose to include two components because of the relatively small sample size of our dataset (n = 65). The first two principal components that emerged from the PCA together accounted for 63% of the total variability in the original data. The first component accounted for 35% of the variability with positive loadings from soil pH, soil moisture, and grass cover and negative loadings for moss, lichen and forb cover. The second component accounted for 28% of the variability in the original variables with positive loadings from soil moisture and grass cover and negative loadings from leaf litter cover and leaf litter depth (Table 6).

The model-averaged overall estimates of occupancy and detection probability of earthworms were, respectively, 0.83 ± 0.07 and 0.68 ± 0.04. Among the impact levels, the occupancy estimate was highest at road sites (0.90 ± 0.09) and lowest at remote sites (0.73 ± 0.16), although confidence intervals of occupancy at all three human impact levels overlapped considerably (Table 7). Earthworms were more likely to occupy hardwood-dominated sites (0.91 ± 0.06) than conifer-dominated sites (0.47 ± 0.16).

The top-ranked occupancy model had a weight of 0.31 and included terms for forest type and distance to roads (Table 8). The second-ranked model, with a weight of 0.16, included terms for forest type and the impact levels boat launch and road distance. The evidence ratio between these two models suggested the highest-ranked model was 1.9 times more likely to be the most parsimonious model than the second-ranked model, but a Δ AICc < 2 indicated that the two models were nearly equivalent (Symonds and Moussalli 2011). In fact, the combination of the road and boat launch terms, both reflecting categories of sites very close to roads, conveyed much of the same information as the distance term.

Forest type was included in all highly-ranked models (importance value of 0.98, Table 9, Table 9). Its value as parameterized (conifer as intercept, hardwood as dummy variable) was consistently positive (95% CI: 0.76, 4.14), meaning that earthworms were more likely to occur under hardwoods than under conifers. Distance to roads

Table 5. Correlation matrix for variables used in principal component analysis. *Correlation is significant at the 0.05 level (2-tailed).**Correlation is significant at the 0.01 level (2-tailed).

	litter cover	moss cover	grass cover	forbs cover	lichen cover	soil pH	soil moisture
moss cover	**-0.39****						
grass cover	**-0.54****	**-0.45****					
forbs cover	-0.12	**0.24***	**-0.28***				
lichen cover	-0.22	**0.51****	**-0.28***	0.01			
soil pH	0.15	**-0.62****	**0.51****	**-0.33****	**-0.47****		
soil moisture	**-0.38****	-0.17	**0.53****	-0.17	**-0.30***	**0.26***	
litter depth	**0.53****	**-0.43****	**-0.24***	-0.18	-0.19	0.00	**-0.26***

Table 6. Factor analysis loadings for components: (n = 65).

Variable	dim1	dim2
litter cover	0.075	-0.905
moss cover	-0.816	0.380
grass cover	0.719	0.566
forbs cover	-0.445	0.082
lichen cover	-0.672	0.185
soil pH	0.823	-0.042
soil moisture	0.517	0.564
litter depth	0.161	-0.780

Table 7. Model-averaged estimates of occupancy (Ψ) and detection probability (p). Uncond. SE: unconditional stand error.

Parameter	Estimate	Uncond. SE	95% CI
Ψ	0.83	0.07	0.63, 0.93
$\Psi_{\text{boat launch}}$	0.84	0.08	0.59, 0.95
Ψ_{road}	0.90	0.09	0.42, 0.99
Ψ_{remote}	0.73	0.16	0.38, 0.94
Ψ_{conifer}	0.47	0.16	0.19, 0.76
Ψ_{hardwood}	0.91	0.06	0.72, 0.97
p	0.68	0.04	0.59, 0.76

was the only other parameter with an importance value greater than 0.5. Even though its model-averaged 95% confidence interval included zero, the parameter estimate for distance to roads was negative in all models in which it was included, indicating that the likelihood of earthworm occurrence decreased with increasing distance from roads.

Table 8. Top five occupancy models for earthworm occurrence based on the AICc. K: the number of estimated parameters.

Model (occupancy)	Log-likelihood	K	AICc	Δ AICc	Akaike weight
hardwood + distance	-111.86	4	232.39	0	0.31
hardwood + boat launch + road	-111.38	5	233.78	1.39	0.16
hardwood + distance + Dim2	-111.7	5	234.42	2.03	0.11
hardwood + distance + Dim1	-111.71	5	234.44	2.05	0.11
hardwood + distance + boat launch + road	-111.22	6	235.88	3.5	0.05

Table 9. Model-averaged parameters on logit scale from models of earthworm occurrence. Estimate: model-averaged parameter estimates. SE: Unconditional standard errors.

Parameter	Importance	Estimate	SE	95% CI
hardwood	0.98	2.45	0.86	0.76, 4.14
distance	0.69	-0.30	0.16	-0.62, 0.02
boat launch	0.37	1.54	1.10	-0.61, 3.69
road	0.37	2.86	1.78	-0.62, 6.34
Dim1	0.26	0.08	0.24	-0.39, 0.55
Dim2	0.26	0.16	0.33	-0.48, 0.8

Effects of earthworm presence on soil properties

The presence of earthworms did not affect leaf litter depth or other measured soil properties. In a two-way MANOVA of the three factors *impact level*, *forest type*, and *earthworm occurrence* on the three dependent variables of *soil pH*, *soil moisture*, and *leaf litter depth*, the combined dependent variables differed among impact levels (Pilliai's trace = 0.804, F= 11.7, $p < 0.001$) and between forest types (Pilliai's trace = 0.243, F = 5.47, $p = 0.002$), but the combined variables did not differ between sites where earthworms were present or absent (Pilliai's trace = 0.037, F = 0.648, $p = 0.588$). Follow-up univariate ANOVA tests and Bayesian model averaging confirmed that neither *soil pH*, *soil moisture*, nor *leaf litter depth* were affected by the presence or biomass of earthworms.

Discussion

Exotic earthworms were found to inhabit 90% of road corridors and 85% of boat launch sites, but only 48% of low impact sites. These results suggest that human traffic influences earthworm presence in the KNWR. Similarly, Cameron and Bayne (2009) found a higher probability of earthworm occurrence at boat launches and roads compared to forest interiors and remote shorelines in Alberta, Canada. Gundale et al. (Gundale et al. 2005) found exotic earthworms at all non-wilderness sites (fishing, timber harvest, road) in Michigan, but at only 50% of wilderness sites with no history of logging.

The road system in the KNWR, while poorly developed compared to conservation units in the contiguous U.S., is fairly extensive compared to other Federal conservation units in Alaska, constituting ~1% of the refuge (100 m buffer either side of all refuge roads gives 6,420 ha). The paved 35 km Sterling Highway and graveled 31 km Skilak Lake Road together bisect the KNWR. These two unpaved roads provide connectivity to many of the 2,900 km of seismic lines (U.S. Fish & Wildlife Service 2010) and three active oil fields that have been laid down on the landscape over the past six decades. Road age has been linked to earthworm presence in northern Alberta, where Cameron and Bayne (2009) found that older road corridors (average age = 46 years) were significantly more likely to have earthworms than younger ones. The few roads on the KNWR were built in the 1950s, suggesting that they likely contributed to the dispersal of exotic earthworms, although sites on Tustumena Lake in the southern KNWR suggest that roads and survey lines are not necessary for earthworm invasion.

We found *Dendrobaena octaedra* to be the most widespread (adults at 70% of study sites) and abundant species (25.6 ± 4.4 ind./m^2) of earthworm on KNWR. This species is most likely introduced and spread by vehicles because its small size and epigeic habits (i.e., inhabit near-surface of the leaf litter) likely increase its chances of dispersal by human activities. *Dendrobaena octaedra* is a prominent invader throughout North America, often both the most widespread and densest exotic earthworm (Cameron et al. 2007).

Dendrodrilus rubidus was found at only two locations geographically distant from each other, suggesting independent introduction events and perhaps multiple vectors. In an unrelated sampling effort, we have also collected *Dd. rubidus* in the subalpine zone on the southern portion of the refuge at a site accessible only by floatplane or by foot (http://arctos.database.museum/guid/KNWR:Ento:7100), again suggesting another independent introduction.

Dendrodrilus rubidus is a fairly common earthworm that appears to be present more in northern hardwood and coniferous forests throughout Alaska and Canada (Cameron et al. 2007, Addison 2008, Costello et al. 2011) than in hardwood forests in the Midwest and other areas of the contiguous United States (Hale et al. 2005, Suárez et al. 2006, Holdsworth et al. 2007b). Like *D. octaedra*, it is tolerant of both acidic conditions and frost and, as an epigeic species, likely impacts the forest floor ecosystems less than anecic species (Addison 2008).

In contrast, *L. terrestris* is an anecic species that lives deep in the soil (Hale et al. 2005, Suárez et al. 2006, Addison 2008) and is commonly sold as fishing bait. We found *L. terrestris* at three boat launches within 5 km of one another, all at lakes popular for sport fishing (Figure 1). This peculiar distribution and the fact that *L. terrestris* is sold for bait locally (e.g, http://arctos.database.museum/guid/KNWR:Ento:6753) suggests direct bait abandonment as the main method of introduction on the KNWR. Additional species may be expected to arrive at boat launches because fishing bait can contain other species as well (Tiunov et al. 2006).

Though we did not detect *L. rubellus* in our sampling effort, it is presently known to occur on KNWR at only one site, a boat launch on a popular fishing lake. As with *L. terrestris*, it was most likely introduced by bait abandonment.

In this study, the most important factors determining earthworm occurrence appeared to be forest type (conifer versus hardwoods) followed by distance from roads. We found that earthworms were more likely to be found at sites dominated by deciduous trees and shrubs than at sites dominated by conifers. On KNWR, conifer dominated sites tend to have acidic soils covered by a thick moss carpet, conditions unfavorable to most earthworm species. In contrast, hardwood sites tend to have less acidic soils covered by deciduous leaf litter, providing more ideal conditions for most earthworm species.

Our finding that half (48%) of the low impact sites (> 600 m from any road or facility, and 50 m from any trail or river) contained earthworms was relatively higher than Cameron and Bayne (2009), who noted 8-35% of their remote transects (300-500 m in the forest interior) contained earthworms, but similar to Gundale et al. (2005) who found 50% of wilderness areas without earthworms. The difference between occurrence patterns in the above studies and KNWR, with its remote sites far from roads supporting earthworms, is perhaps due to boat and float plane access into more remote regions of the KNWR. Similarly, Holdsworth et al. (2007b) found that of all habitat and distance variables, distance to roads was the only significant predictor of earthworm occurrence in a Wisconsin hardwood forest for most earthworm groups. Holdsworth et al. (2007b) noted that *Dendrobaena* species are early colonizers among earthworm assemblages. The highest occurrence of *Dendrobaena* near roads suggests that the KNWR may be in the early stages of earthworm colonization.

Besides surface vehicle access, other anthropogenic influences likely contribute to earthworm presence in KNWR, especially in more remote areas. These remote site invasion vectors are not easily identified. *Dendrobaena octaedra* was found throughout the study area, most likely introduced by road construction, but also possibly by seismic exploration, fire suppression activities, and mechanical tree crushing for moose browse in the northern part of the KNWR during the 1970s. There, extensive seismic lines, mostly in the northern part of the Refuge, have been in place since as early as the 1950s, and many remain visible on the landscape today as animal, hiking, and snowmobile trails, as well as illegal access routes for all-terrain vehicles (U.S. Fish & Wildlife Service 2010). Numerous prescribed fires and wildfires within the KNWR, together with associated control and suppression efforts using heavy equipment, provided additional opportunities for earthworm establishment.

There are also non-anthropogenic vectors that can spread earthworms such as birds (D. Saltmarsh, *pers obs.*) and streams. In southeast Alaska, Costello et al. (2011) found that earthworms appear to disperse along streams. They showed that several earthworm species could survive ≥ 6 days submerged in a stream.

Factors such as soil pH likely also limit earthworm distribution. Most earthworms prefer soil pH of 5–7.4 (Addison 2008). While earthworms were found in the present study at sites with slightly higher pH (5.74 ± 0.13, n = 48 sites) than sites without earthworms (5.32 ± 0.23, n = 21), the distribution observed was most likely due to the distance from human impacts rather than pH. The average pH of the low impact sites was significantly different from other site types, likely due to the high number of low

impact sites dominated by conifers compared to boat launch and road sites. Addison (2008) cited references documenting earthworms under fairly acidic conditions: *D. octaedra* has been found in areas of Canada with a pH as low as 2.8-3.6; *Dd. rubidus* and *L. terrestris* have been recorded in areas with pH of 3.0-3.4, suggesting that even low impact sites on KNWR were well within the range of tolerance for both species.

Earthworm densities showed substantial variation with a mean value (28 earthworms/m^2) comparable to other studies. Cameron et al. (2007) found densities along transects in Alberta of 0-35 earthworms/m^2, averaging 2-41 earthworms/m^2. González et al. (2003) found average density in a Colorado aspen forest was 44.4 earthworms/m^2. Boat launches had the highest density of earthworms, likely due to introduction from both roads and bait abandonment, as well as close proximity to campgrounds (Cameron et al. 2007).

We found no evidence that earthworms were affecting the soil properties pH, soil moisture, and leaf litter depth on KNWR. Likely explanations are the dominance of the epigeic *D. octaedra*, moderate densities of earthworms, and that these may have been young infestations. In Minnesota, Hale et al. (2005) found that the *Dendrobaena* group alone did not remove the forest floor or change other soil parameters, while *L. terrestris* resulted in the complete removal of surface litter and the lowest percentage of organic matter in the A horizon. They also found that fine root density, total fine root biomass, and nutrient availability were lower in *L. terrestris* dominated areas compared to others. These observations in other systems suggest that *D. octaedra* has a lesser impact on forest floor ecology than *L. terrestris*, so ecological impacts may not be apparent within the *D. octaedra* dominated KNWR. Moderate densities and biomass of earthworms as well as the potential that these populations have not had many years to work the soil are additional reasons that they have not yet measurably altered soil properties on KNWR.

In temperate studies, earthworm invasions appear to follow a predictable successional sequence, beginning with early invasion by epigeic species, such as *D. octaedra*, and epi-endogeic species, like *L. rubellus.* Subsequently endogeic and anecic species like *L. terrestris* colonize (Hale et al. 2005, Tiunov et al. 2006, Addison 2008). Gundale et al. (2005) confirmed this sequence in Michigan where they found communities consisting of just one or two species that were almost exclusively composed of *D. octaedra* and *L. rubellus.* This was similarly observed by Suárez et al. (2006) in New York where the edge of earthworm distribution was dominated by *L. rubellus*, followed by communities dominated by *L. terrestris.* This sequence can largely be explained by the differences in species traits such as reproductive strategy, fecundity, cold tolerance, and colonization rates. *D. octaedra* is partheogenic, has high cocoon production (Dymond et al. 1997), is extremely frost tolerant and can withstand over-winter freezing in all stages of development down to at least -14 °C. Together, these traits in *D. octaedra* aid in its success as an initial invader (Holmstrup 1994, Bindesbøl et al. 2007).

Even though differences in cold tolerance do limit the distributions of earthworm species at larger scales (Meshcheryakova et al. 2014), the extent our study area, confined to the central lowlands of the western Kenai Peninsula, did not cover enough of a climatic gradient for consideration of temperature as a determinant of earthworm invasion success.

Regionally in Alaska, the distribution of permafrost and cold winter temperatures, as well as soil moisture and pH, likely limit earthworms' potential Alaskan distribution. Where earthworms can survive, historic and current human activity and land use practices, and the composition of particular source populations, likely determine earthworm occurrence. The fact that all earthworm records in Alaska up to the present time have been from southern Alaska (see Suppl. material 1: Alaska earthworm records) despite rates of earthworm introductions that are likely comparable in southern and Interior Alaska indicates that the harsher, colder climate of the Interior precludes successful invasions by most earthworms. However, some of the more cold-hardy species present in the far north of the Palearctic, including *D. octaedra* and *Dd. rubidus*, may be able to survive in Interior Alaska based on the physiological and distributional data presented by Meshcheryakova et al. (2014).

Both *D. octaedra* and *Dd. rubidus* are parthenogenic, frost-hardy species, traits that, combined with their ability to tolerate acidic soils and exploit poor litter quality, contribute to their success in colonizing large areas. As with many "weedy" species, parthenogenesis facilitates rapid reproduction from very low densities, characteristic of rare dispersal events, where a single individual can establish an entire population (Tiunov et al. 2006). The small body size of these species also facilitates spread by vectors such as tires more often than *Lumbricus* and other anecic species. Given its wide distribution on the KNWR and its particular ecological traits, *D. octaedra* will likely be able to colonize large areas of permafrost-free Alaska, an expanding region as climate warms (Osterkamp 2005). While *D. octaedra* has limited impacts compared to other exotic earthworm species, its presence could portend an invasion by a larger assemblage of earthworms and commensurate changes in soil properties if Alaska follows the same colonization sequence seen elsewhere in northern North America.

Conclusion

As there are no effective strategies for removing exotic earthworms once they are established, preventing invasion and slowing their dispersal are the only viable ways to reduce their overall impacts. While we found that *D. octaedra* was widespread, most of the KNWR was free of the more damaging *Lumbricus* species. Most of the KNWR can be kept free of *Lumbricus* species for many years due to the extremely slow natural dispersal rate of these worms. Because the main vectors of earthworms on the KNWR appeared to be vehicles and bait abandonment, logical methods for slowing the spread of species already on the landscape and preventing the introduction of additional earthworm species would be to minimize vehicular activity in areas currently devoid of earthworms and to explicitly prohibit the use of earthworms as live bait.

As the first study of earthworm diversity and distribution in the southcentral Alaska region, we established patterns of distribution likely to hold true regionally and we set the stage for considering ways to limit the further introductions of exotic earthworms in Alaska.

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Supplementary material 1

Alaska earthworm records

Authors: Deanna Marie Saltmarsh, Matthew L. Bowser, John M. Morton, Shirley Lang, Daniel Shain, Roman Dial

Data type: occurrence

Explanation note: Earthworm records from Alaska exclusive of data from the present study are compiled. All literature items cited are included in the References section of the manuscript.

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Supplementary material 2

Specimen records

Authors: Deanna Marie Saltmarsh, Matthew L. Bowser, John M. Morton, Shirley Lang, Daniel Shain, Roman Dial

Data type: occurrence

Explanation note: Occurrence data are provided for earthworm specimens collected. Data field definitions are those used by Arctos (http://arctos.database.museum/, http://arctosdb.org/).

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Supplementary material 3

Analysis dataset

Authors: Deanna Marie Saltmarsh, Matthew L. Bowser, John M. Morton, Shirley Lang, Daniel Shain, Roman Dial

Data type: measurement

Explanation note: This spreadsheet file contains all original measurements and derived metrics used in the analyses. It is arranged in a relational format. The sheet labeled site_data contains all site-level data, including original data and some derived metrics; the plot_data sheet contains plot-level data. The earthworm_lengths sheet contains all of the earthworm length measurements and, by implication, the occurrence data. The two response_data sheets hold data derived from the first three sheets that were used in subsequent analyses.

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